Palaeogeography, Palaeoclimatology, Palaeoecology 505 (2018) 63–72

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Controls of climate, catchment erosion and biological production on long-term community and functional changes of chironomids in High Arctic lakes (Svalbard)

Tomi P. Luoto[a,*], Antti E.K. Ojala[b]

[a] Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Niemenkatu 73, FI-15140 Lahti, Finland
[b] Geological Survey of Finland, Betonimiehenkuja 4, FI-02150 Espoo, Finland

ARTICLE INFO

Keywords:
Biodiversity
Chironomids
Climate change
Functional traits
Paleoecology
Polar lakes

ABSTRACT

Arctic freshwater basins are diversity hotspots and sentinels of climate change, but their long-term variability and the environmental variables controlling them are not well defined. We examined four available lake sediment sequences from High Arctic Svalbard for their subfossil Chironomidae communities, biodiversity and functional traits and assessed the influence of climatic and limnological variability on the long-term ecological dynamics. Our results indicated that collector-filterers had an important role in the oligotrophic sites, whereas collector-gatherers dominated the nutrient-enriched sites with significant bird guano inputs. In the oligotrophic sites, benthic production, taxon richness and taxonomic and functional diversity were highest during the early Holocene, when temperatures showed a rapid increase. An increase in subfossil abundance and diversity metrics was also found in recent samples of the oligotrophic sites, but not in the bird-impacted sites, where the trends were decreasing. When partitioning out the environmental forcing on chironomid communities, the influence of climate was significant in all the sites, whereas in-lake production (organic matter) was significant in two of the sites and catchment erosion (magnetic susceptibility) had only minor influence. The findings suggest that major changes in Arctic chironomid assemblages were driven by climate warming with increasing diversity in oligotrophic sites, but deteriorating ecological functions in environmentally stressed sites. We found that although taxonomic and functional diversity were always coupled, taxonomical and functional turnovers were coupled only in the oligotrophic sites suggesting that the ecological functions operated by chironomids in these low-productivity sites may not be as resilient to future environmental change.

1. Introduction

A significant portion of inland biodiversity in the Arctic is found in freshwater lakes (Rautio et al., 2011). However, ongoing climate warming, which has amplified impacts in the Arctic (Serreze and Barry, 2011; Linderholm et al., 2018) is altering the balance of aquatic communities by rates already exceeding natural variability (Smol and Douglas, 2007). Although it is well-documented that aquatic communities have been increasingly changing in the Arctic (Wrona et al., 2016), less is known about the variability between different types of freshwater systems or limnoecological functioning, especially at long temporal scales. In addition, understanding long-term climate impacts on Arctic lake ecosystems requires separating the effects of climate from within-lake and catchment changes over a long time span (Paull et al., 2017). The paleolimnological approach to studying long-term limnoecological changes provides powerful means of examining ecological shifts and the environmental history of lakes, giving insights into past and present dynamics, but also offering an opportunity to forecast future changes in aquatic environments (Smol, 2010; Pla-Rabes et al., 2011). However, only few quantitative palaeolimnological studies have addressed biodiversity questions, defining the drivers of change in species richness or identifying functional traits that best capture ecosystem processes (Gregory-Eaves and Beisner, 2011; Nevalainen et al., 2018).

Paleoecological research has traditionally focused on using communities as the main unit, since many aquatic organism groups that are well preserved as subfossils, such as diatom algae, Cladocera zooplankton and Chironomidae macrobenthos, respond sensitively to environmental perturbation through community changes (Frey, 1988). Although the potential of using functional traits to characterize long-term aquatic ecosystem changes has been known (Jeppesen et al., 2001) it has gained more interest only recently (Fournier et al., 2015;

* Corresponding author.
E-mail address: tomi.luoto@helsinki.fi (T.P. Luoto).

https://doi.org/10.1016/j.palaeo.2018.05.026
Received 1 February 2018; Received in revised form 16 April 2018; Accepted 18 May 2018
Available online 23 May 2018
0031-0182/ © 2018 Elsevier B.V. All rights reserved.

Nevalainen et al., 2015a, 2015b; Nevalainen and Luoto, 2017). Since ecosystem functions rely more on the living habits of organisms than taxonomic categories, the use of functional traits may enable the assessment of ecosystem functioning and stability more comprehensively than traditional taxonomic identification (Cadotte et al., 2011). Benthic invertebrates, including chironomids, have vital functions in lakes operating crucial biogeochemical cycles behind food-web structure by taking part in processes related to detrital decomposition, nutrient release and transfer, prey control and food supply (Palmer et al., 1997; Covich et al., 1999), for example. While being invaluable for lake functions, benthic insect larvae can be the most threatened organisms in lakes (Strayer and Dudgeon, 2010).

For chironomids, the most useful functional traits for ecological studies are related to their feeding habits (Pinder, 1986; Schmera et al., 2017). Although chironomids tend to vary in their modes of feeding depending on their life cycle stage (Grey et al., 2004), their primary feeding preferences can be divided into eight guilds: collector-filterers, collector-gatherers, predators, scrapers, shredders, parasites, omnivores and piercers (Merritt and Cummins, 1996). Collector-gatherers (deposit-feeders) are the most common feeding guild that depends on fine particulate organic matter of sediments. Another common guild, collector-filterers, which often live in tubes, are suspension feeders filtering food particles from the water column, epiphytic algae being the most common food item (Berg, 1995). Among the less dominant guilds, scrapers shear food material from the sediment and submerged rocks, vegetation and wood, whereas shredders feed on coarse particulate organic matter, such as living vascular plants, submerged wood, macro- or colonial algae, or leaf litter (Berg, 1995). Predators on the other hand attack other invertebrates and ingest all part of the prey (engulfers) or pierce the tissues and withdraw the fluids of the prey (piercers) (Cummins, 1973). In paleolimnology, the thus far rarely used chironomid functional feeding characteristics or their paleo-diets estimated through stable isotopic compositions from head capsules (van Hardenbroek et al., 2014; Belle et al., 2017; Schilder et al., 2017) can be used to provide valuable information on past food web structures, biogeochemical cycling or environmental controls.

Previous studies (Brooks and Birks, 2004; Nevalainen et al., 2012) have revealed significant ecological changes in High Arctic lakes in Svalbard, which is located in an intersection of major oceanic currents and is a focal point for the development of the Polar Front (Majewski et al., 2009). Hence, Svalbard represents a climatically and oceanographically sensitive region (Isaksen et al., 2007). Building from previous studies with available chironomid taxonomic biostratigraphies, in this study, we analyze chironomid functional traits (feeding guilds) and compare the findings against independent air temperature reconstructions, sediment organic matter content and magnetic susceptibility measurements. Our analysis has the potential to provide new knowledge on the influence of climate and limnology on High Arctic ecosystem changes at long temporal scales (decades to millennia). More particularly, we test chironomid paleobiodiversity changes in relation to natural variability caused by sudden short-term catchment originated "pulse events" and in relation to long-term climatic "press events" (Massaferro and Corley, 1998). Furthermore, in wetland ecosystems species turnover across environmental gradients is restricted to functionally similar species, i.e. taxonomic and functional turnover are decoupled, which may allow maintaining ecosystem functioning when subject to future environmental change (Robroek et al., 2017). Here, we test this general theory in four High Arctic aquatic ecosystems with different environmental characteristics including typical low-nutrient tundra sites and nutrient-enriched bird-impacted sites with densely vegetated catchments.

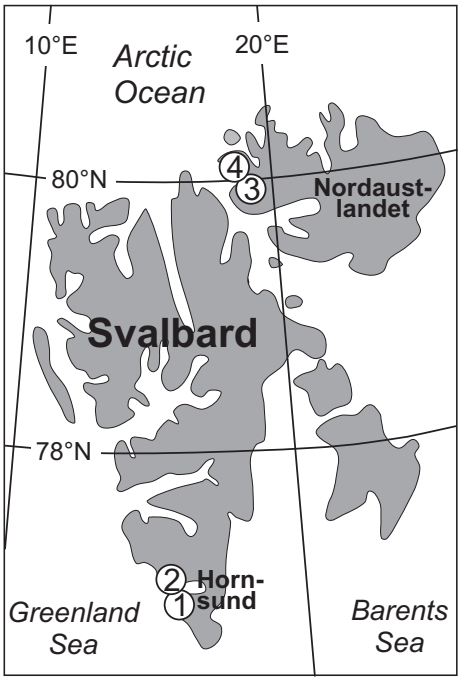

Fig. 1. Study sites. Lakes 1) Svartvatnet, 2) Fugledammen, 3) Einstaken and 4) Kvalroslaguna in Hornsund and Nordaustlandet, High Arctic Svalbard.

2. Material and methods

2.1. Study sites

The four study sites are located in southern (Hornsund fjord area, mean July air temperature 4.2 °C) and northeastern (Nordaustlandet, mean July air temperature 2 °C) Svalbard (Fig. 1). Svartvatnet (76°90′N, 15°68′E; 63 m a.s.l.) is an oligotrophic 80 ha lake located at the southern side of the Hornsund fjord, whereas Fugledammen (77°00′N, 15°52′E; 15 m a.s.l.), located at the northern side of the fjord, is a shallow (2 m) nutrient-rich pond (2 ha). Einstaken (79°58′N; 18°42′E, 54 m a.s.l.) is situated in the Murchisonfjorden area at the southern side of the Isvika bay in Nordaustlandet. The 5 ha lake is currently oligotrophic and has a depth of 8 m. The fourth study site, Kvalroslaguna (79°58′N, 18°34′E; 12 m a.s.l.), is a shallow (1 m) nutrient-rich pond (0.5 ha), located at the northern side of the Isvika bay. Einstaken and Svartvatnet are pristine periglacial basins, whereas Fugledammen and Kvalroslaguna have significant grazing and nesting bird-influence in their catchments. At both sites, birds are present in high numbers and produce a large amount of guano, which is high in nutrients, resulting in thick moss growth in the catchment and giving a murky eutrophic appearance to the ponds. Detailed description of catchment and limnological characteristics can be found from previous publications (Luoto et al., 2011, 2014, 2015, 2016, 2018).

2.2. Sediments and subfossil analyses

Samples consist of two long sediment cores (sampled with a Livingstone piston corer) from Einstaken (134 cm, past ~13,000 years) and Svartvatnet (164 cm, past ~5500 years) and two short cores (sampled with a Russian peat corer) from Fugledammen (100 cm, past ~150 years) and Kvalroslaguna (28 cm, past ~400 years). The cores from Einstaken and Kvalroslaguna were collected during the 2009 field campaign in Nordaustlandet (Kinnvika project) and the Svartvatnet and Fugledammen cores during the 2013 field campaign in Hornsund (QUAL project). The chronologies of the sediment profiles have been previously published (AMS ^{14}C, paleomagnetic, ^{137}Cs and ^{210}Pb dating), alongside analyses of organic matter content (measured as loss

on ignition, LOI), measurements of magnetic susceptibility and the original chironomid stratigraphies for Einstaken (Luoto et al., 2011), Svartvatnet (Luoto et al., 2018), Fugledammen (Luoto et al., 2015) and Kvalroslaguna (Luoto et al., 2014). The Svartvatnet chronology was originally published in Ojala et al. (2016). Subfossil chironomid analyses were performed from 1 cm^3 subsamples using standard methods using the same taxonomy between the cores (Brooks et al., 2007). For this study, the chironomid subfossils handpicked from a Bogorov counting tray were further analyzed for their feeding habits characterizing functional attributes (Schmera et al., 2017). The feeding guilds were based on classifications by Merritt and Cummins (1996) and Mandaville (2002). Chironomid abundance, measured as head capsules per 1 g dry sediment weight, was used as a measure for benthic production (Itkonen et al., 1999; Fortin and Gajewski, 2010).

2.3. Numerical analyses

Taxonomic diversity (mostly species type level) was assessed using number of taxa (taxon richness, S) and Shannon index (H′) (Shannon, 1948) based on a consistent number of examined specimens (50–60) per sample. Functional diversity (FD) was based on the Shannon index of the relative abundances of feeding guilds (Schleuter et al., 2010). Detrended correspondence analysis (DCA) was used to indicate beta diversity (turnover) of chironomid taxa assemblages (Correa-Metrio et al., 2014). The DCAs were run using square-root transformed species data with rare species downweighted. Redundancy analysis (RDA) was used to partial out the contribution of forward selected environmental variables (air temperature, organic matter, magnetic susceptibility) on chironomid taxa assemblages in the four study sites. The RDAs were run with square-root transformed species data, downweighing of rare species and 999 permutations. Air temperature was considered as a proxy for climate influence, organic matter for lake productivity (Meyers and Teranes, 2002) and magnetic susceptibility for physical changes related to catchment erosion and sediment delivery into the basins (Dearing, 1999). The statistical analyses were carried out using the program Canoco 5 (Šmilauer and Lepš, 2014).

The temperature timeseries for the long profiles was the diatom-inferred (weighted averaging-partial least squares technique) North Atlantic August temperature variability (Icelandic core MD99-2269, Sundqvist et al., 2014) and for the short profiles the 2000-year synoptic Arctic air temperature variability (PAGES Arctic 2 k, McKay and Kaufman, 2014). The prediction error of the North Atlantic temperature reconstruction is ± 0.9 °C (95% confidence level), whereas the Arctic temperature variability (no prediction error estimate available) is averaged from a standardized database of several proxy temperature records including tree ring, marine and lake sediment, glacier ice, historical and speleothem data archives. The temperature records were fitted to the chronologies (samples) of this study to match the time resolution using record mean surface air temperature anomalies. However, it should be noted that due to local features in climate variability and inherent uncertainties in chronological matching, the temperature records should be considered tentative.

3. Results

Collector-filterers dominated the chironomid compositions in Einstaken (Fig. 2), *Micropsectra radialis*-type being the most abundant between ~13,000 and 2000 cal yr BP and *Micropsectra insignilobus*-type during the past ~2000 years. Also *Paratanytarus austriacus*-type was common throughout the sequence. Collector-gatherers, such as *Oliveridia* and *Orthocladius* (*P.*) *consobrinus*-type, were common from 13,000 to 7000 cal yr BP and during the last ~2000 years. Also predators, including *Procladius* and *Thienemannimyia*-type, occurred in the record between ~12,000 and 2000 cal yr BP.

In Svartvatnet (Fig. 3), collector-filterers, such as *M. radialis*-type and *Micropsectra contracta*-type dominated from the beginning of the record at ~5500 cal yr BP until 1000 cal yr BP. In the most recent sediment layer, yet another *Micropsectra* species, *M. junci*-type, became abundant. Collector-gatherers, mostly *Orthocladius trigonolabis*-type, *Hydrobaenus lugubris*-type and *Oliveridia*, had an increasing trend in their relative proportion from ~5500 cal yr BP reaching maximum abundances between ~3000 and 500 cal yr BP. Predators (*Procladius*) occurred in the record between ~5500 and 3500 cal yr BP and shredders (*Cricotopus cylidraceus*-type) occasionally from 2000 cal yr BP onwards.

The chironomid compositions in Fugledammen (Fig. 4) were almost monotonously dominated by collector-gatherers, with *Psectrocladius sordidellus*-type being the most abundant between ~1840 and 1870 CE and *O. consobrinus*-type from ~1880 CE until the present, when it reached total dominance. The only non-collector-gatherer in the record was the shredder *Cricotopus* (*I.*) *intersectus*-type that occurred in the two lowermost samples between ~1840 and 1850 CE.

Collector-gatherers were also the dominant feeding guild throughout the record in Kvalroslaguna (Fig. 5) with *P. sordidellus*-type and *Metriocnemus eurynotus*-type as the most abundant taxa. *Hydrobaenus conformis*-type was abundant in the initial part of the record between ~1620 and 1660 CE, whereas *Chironomus anthracinus*-type increased from ~1880 CE onwards. Predators (mostly *Procladius*) appeared in the record at ~1700 CE and shredders at ~1880 CE (*Cricotopus*), although with low abundances.

Excluding the first 1000 years, organic matter, subfossil abundance (benthic production), taxon richness, Shannon index and functional diversity were generally higher in the initial part of the Einstaken record (Fig. 6) and lower in the latter part from ~7000 cal yr BP onwards. However, a slight general increase in benthic production, DCA axis 1 scores and diversity parameters, concurrent with increases in magnetic susceptibility, was apparent during the past ~2000 years. In Svartvatnet (Fig. 7), magnetic susceptibility and organic matter showed no notable trends, except in the most recent centuries when magnetic susceptibility reached the lowest and organic matter highest values in the record. Subfossil abundance and the diversity parameters had higher values in the later part of the record (past ~2000 years), contrasting the DCA axis 1 scores, however with lower values around 500 cal yr BP. The organic matter content showed a progressive increase throughout the record in Fugledammen (Fig. 8). In contrast, magnetic susceptibility, subfossil abundance and diversity parameters showed a progressively decreasing trend towards the present that was also apparent in the DCA axis 1 scores. The patterns in Kvalroslaguna (Fig. 9) were similar to Fugledammen, however, the patterns in taxon richness and functional diversity remained less clear.

Taxonomic diversity correlated significantly with functional diversity in all the study sites (Fig. 10) with the combined data having an R^2 of 0.32 ($P < 0.001$). The oligotrophic sites (Einstaken and Svartvatnet) had a stronger correlation ($R^2 = 0.54$, $P < 0.001$) than the bird-impacted sites (Fugledammen and Kvalroslaguna), which nonetheless also had significant relationship ($R^2 = 0.20$, $P < 0.001$).

In the DCAs, the variance explained by the first and second axes in Einstaken were 29.4% and 16.6%, in Svartvatnet 31.5% and 21.3%, in Fugledammen 36.4% and 23.3% and in Kvalroslaguna 28.3% and 17.7%, respectively. The DCA axis 1 and 2 scores are shown in Figs. 6–9. Due to intermediate gradient lengths in the initial DCAs (2.4–2.6 SD), RDA was selected to partial out variance of forward selected environmental variables on chironomids. Temperature, organic matter and magnetic susceptibility explained 30.8% of all variance in Einstaken, 10.1% in Svartvatnet, 31.8% in Fugledammen and 27.4% in Kvalroslaguna. Temperature was a significant explanatory factor ($P \leq 0.05$) on chironomid community dynamics in all the study lakes, whereas organic matter had significant influence in Einstaken and Kvalroslaguna and magnetic susceptibility only in Einstaken (Table 1). In all, although the examined variables explained a relatively small portion of the total variance, the RDA results generally suggest that the influence of climate and biological production on chironomids has been

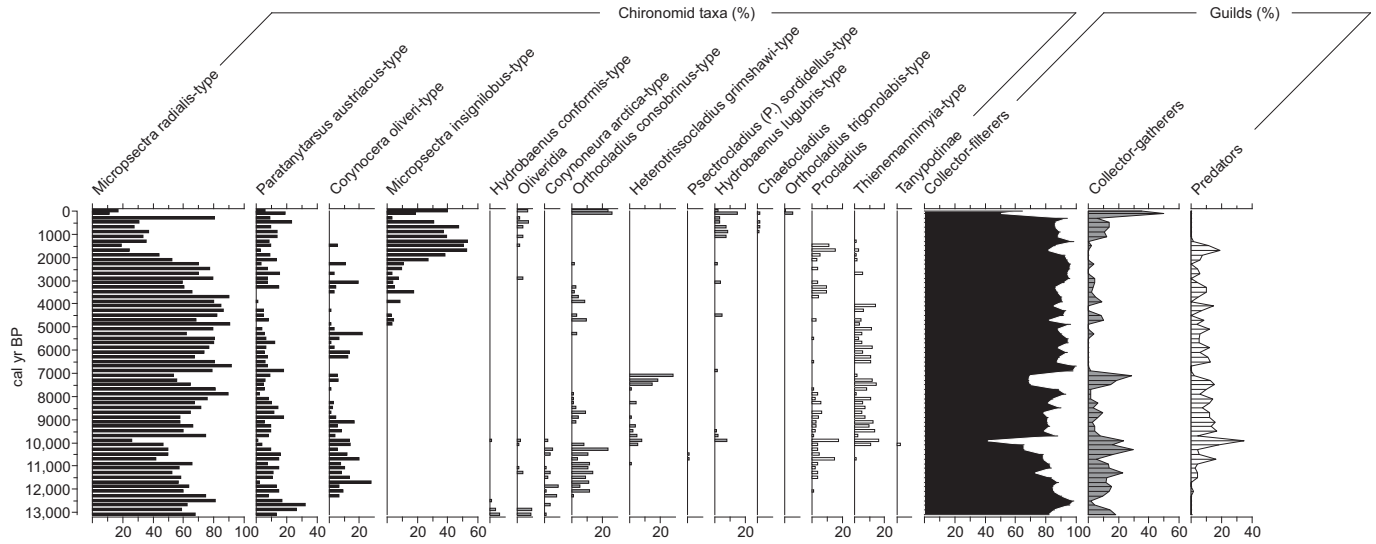

Fig. 2. Einstaken biostratigraphy. Relative taxa abundances (originally published in Luoto et al., 2011) and feeding guilds of chironomids in the Einstaken sediment record. The shading of the taxa refers to the shading of the associated feeding guild.

significant in the study lakes, whereas the influence of catchment erosion has been less important.

4. Discussion

4.1. Functional ecology

The transparent oligotrophic study sites Einstaken (Fig. 2) and Svartvatnet (Fig. 3) with no significant catchment vegetation were dominated by collector-filterers. On contrast, collector-filterers were completely absent in the nutrient-rich bird-impacted sites Fugledammen (Fig. 4) and Kvalroslaguna (Fig. 5), which were dominated by collector-gatherers. Arctic birds that feed in the Ocean and nest on lake catchments transport nutrients (P, N) from the marine to the terrestrial realm (Keatley et al., 2009). These nutrients stored in bird guano are delivered directly or by surface runoff to coastal lakes and ponds (Keatley et al., 2009). Potentially, bird-driven nutrient enrichment of Arctic lakes will alter the limnoecological functions, which are reflected through, for example, chironomid feeding habits. According to multiproxy results, the oxygen conditions in Fugledammen deteriorated at the end of the 19th century (Luoto et al., 2015) causing for example a decrease in chironomid diversity. In Kvalroslaguna, the bird-induced increase in nutrients appears to have begun already during the 18th century based on the oxygen preferences of chironomids (Luoto et al., 2014). Comparison of the study sites show that the relative significance of collector-gatherers fully corresponds with the level of bird-impact. This is most likely related to the benthic requirements of collector-filterers (Liu and Wang, 2008) that cannot succeed in the murky low-oxygen bird-impacted sites. This is not a phenomenon related only to the Arctic, since collector-gathers (detritivores) appear to dominate eutrophic sites also in boreal areas, while collector-filterers are absent or rare at these sites (Luoto and Ojala, 2014).

If organic inputs to the sediment are not in balance with the decomposition capacity, the functioning and biodiversity of lake ecosystems will be radically altered resulting in degradation of water quality (Palmer et al., 1997). In general, the current results are logical in the sense that collector-gatherers prefer high organic matter contents and shallow nutrient-rich waters, whereas collector-filterers favor lower organic matter content and oligotrophic waters with intermediate depth suggesting control of benthic and pelagic production, respectively. Hence, the present results appear to confirm our previous findings where the presence of the collector-feeding lifestyle of chironomids

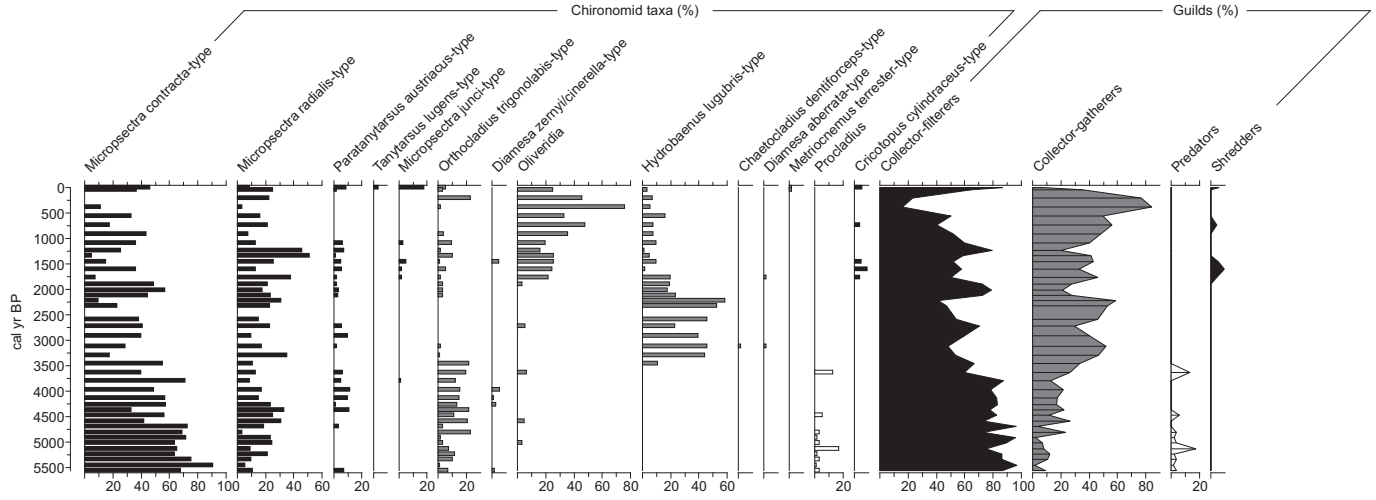

Fig. 3. Svartvatnet biostratigraphy. Relative taxa abundances (originally published in Luoto et al., 2018) and feeding guilds of chironomids in the Svartvatnet sediment record. The shading of the taxa refers to the shading of the associated feeding guild.

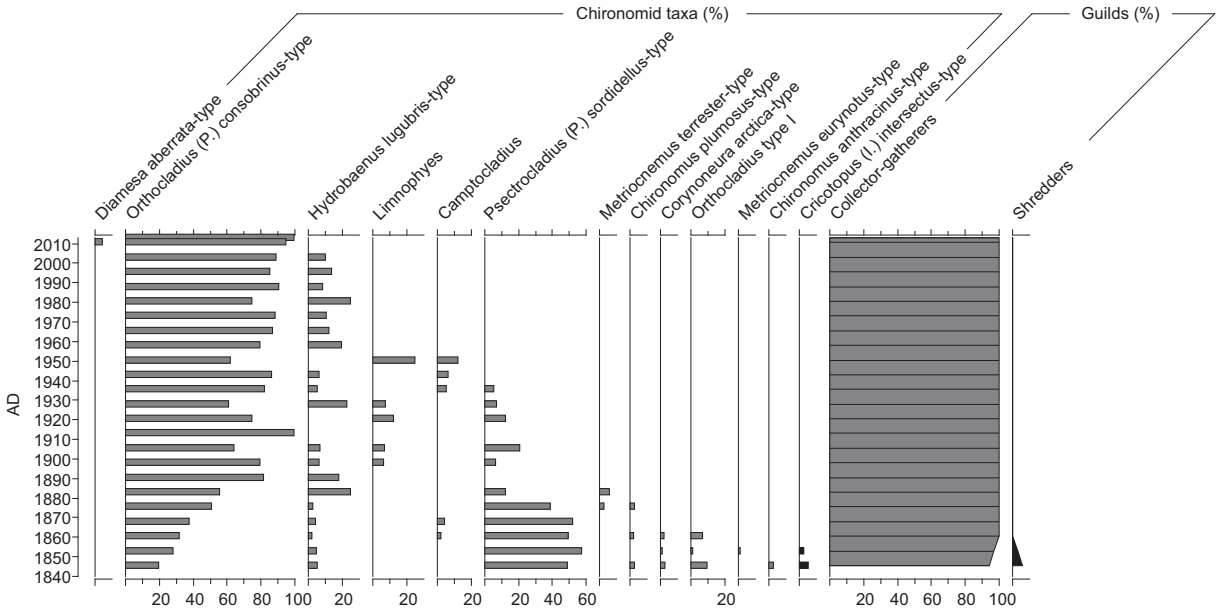

Fig. 4. Fugledammen biostratigraphy. Relative taxa abundances (originally published in Luoto et al., 2015) and feeding guilds of chironomids in the Fugledammen sediment record. The shading of the taxa refers to the shading of the associated feeding guild.

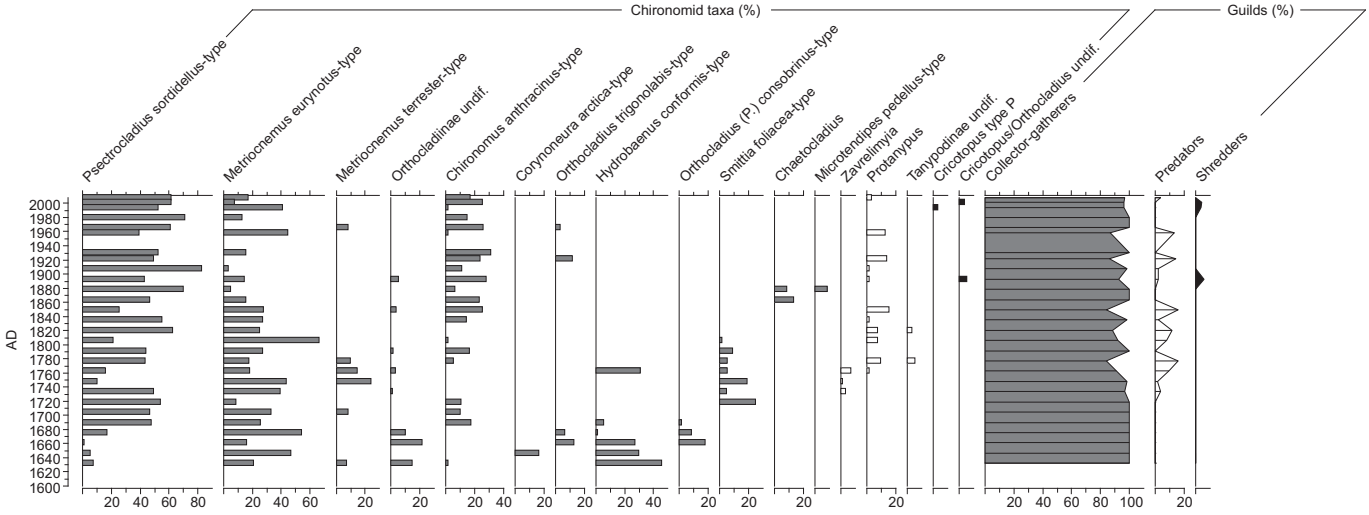

Fig. 5. Kvalroslaguna biostratigraphy. Relative taxa abundances (originally published in Luoto et al., 2014) and feeding guilds of chironomids in the Kvalroslaguna sediment record. The shading of the taxa refers to the shading of the associated feeding guild.

characterized a functionally diverse community and a healthy pre-disturbance aquatic ecosystem state (Luoto and Ojala, 2014).

Although benthic functions are related to inlake factors that regulate habitat characteristics and food availability (Vadeboncoeur et al., 2002), they are also related to external processes, such as climate. It has been shown from Finnish lakes that at both spatial and long-term temporal scales the relative importance of chironomid feeding guilds fluctuates alongside climate characteristics (Luoto and Nevalainen, 2015). Under cold climate conditions and during cold climate events of the Holocene, such as the early Holocene and the Little Ice Age, collector-filterers tend to dominate, whereas under warm and intermediate climate conditions and similar climate episodes of the past, collector-gatherers, shredders, scrapers and predators have more important roles (Luoto and Nevalainen, 2015). In the current results, similar climate-driven temporal patterns are not clear. Only in Einstaken which is the most oligotrophic site, collector-gatherers increase at the expense of collector-filterers during the recent climate warming (Fig. 2). Whereas the temporal changes in the bird-impacted sites have remained minute (Figs. 4, 5), possibly partly related to shorter chronological time span, a distinct shift has occurred in Svartvatnet, where collector-gatherers gradually increased (Fig. 3). Instead of a response to climate, it is more likely that this is related to catchment originated increase in nutrient inputs, which is demonstrated by the decreasing magnetic susceptibility values (Fig. 7) suggesting physical catchment control (Royall, 2001).

4.2. Biodiversity

Changes in taxon richness and taxonomic and functional diversity appear site-specific in the studied lakes. In the longest record, Einstaken, diversity peaks during the early Holocene following the thermal maximum at ~10,000 cal yr BP (Fig. 6), a diversity trend also found in records from continental Northern Europe (Shala et al., 2014). Similarly, concurrent with the present climate warming, the diversity indices showed increases in the most recent sediment layers suggesting that chironomid assemblages and functional behavior are most diverse during warmer climate conditions (Levesque et al., 1996; Burgmer

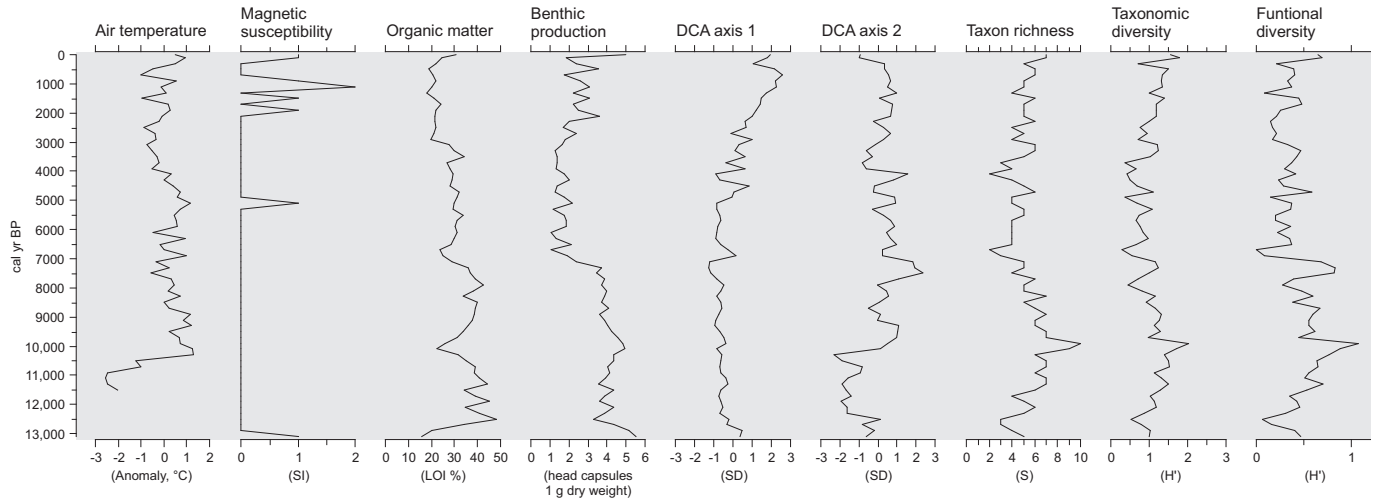

Fig. 6. Einstaken record. North Atlantic temperature variability (Sundqvist et al., 2014), magnetic susceptibility and organic matter content (measured as loss on ignition) of the sediment compared with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes scores, taxon richness, taxonomic diversity (Shannon index, H′) and functional diversity of chironomids in the Einstaken sediment record.

et al., 2007). In addition, the accumulation of chironomid subfossil head capsules, indicating benthic production (Itkonen et al., 1999; Fortin and Gajewski, 2010), has been high during the early Holocene and the most recent period. The Svartvatnet record is less clear, but showed a similar increase in benthic production and taxonomic richness and diversity during the most recent times. The results thus confirm previous evidence that favorable climate conditions support habitat availability and diversity to a certain extent (Schindler and Smol, 2006).

Benthic production, taxon richness and taxonomic and functional diversity decreased in Fugledammen alongside climate warming since the Little Ice Age (Fig. 8) in contrast with the oligotrophic sites. Although not as clear as in Fugledammen, taxon richness and diversity also decreased in Kvalroslaguna. In all the records, although not synchronous, organic matter content tended to follow air temperature dynamics, as biological production is known to be temperature dependent (Meyers and Lallier-Verges, 1999). The diversity changes more or less tracked the changes in organic matter in the study sites, so that in the oligotrophic sites organic matter and diversity had positive relationship, and in the bird-impacted sites the relationship was negative. This fits well with the general observations on invertebrate biodiversity patterns in freshwaters that diversity increases along biological production until a limnological threshold, after which diversity begins to decrease (Nyman et al., 2005; Luoto, 2011; Jensen et al., 2013). Variability in magnetic susceptibility also reflects climate oscillations to some extent. The majority of magnetic minerals found in these sediments are magnetite of different grain sizes that are delivered into lakes by catchment erosion and originate from bedrock, subsoil, and topsoil in the lake's drainage. This process is enhanced by climatic factors including temperature and precipitation (Sandgren and Snowball, 2002). The changes in magnetic susceptibility are not easily connected with changes in chironomid taxonomic or functional diversity in the oligotrophic sites, but in the impacted sites there were increases in the diversity indices with decreasing magnetic susceptibility towards the present day.

Reductions in chironomid paleobiodiversity have been shown to be related to natural variability caused by sudden short-term catchment “pulse events” in water turbidity and long-term climatic “press events” (Massaferro and Corley, 1998). During pulse disturbances (e.g. hydrological events), diversity has a tendency to fall, but recover rapidly after

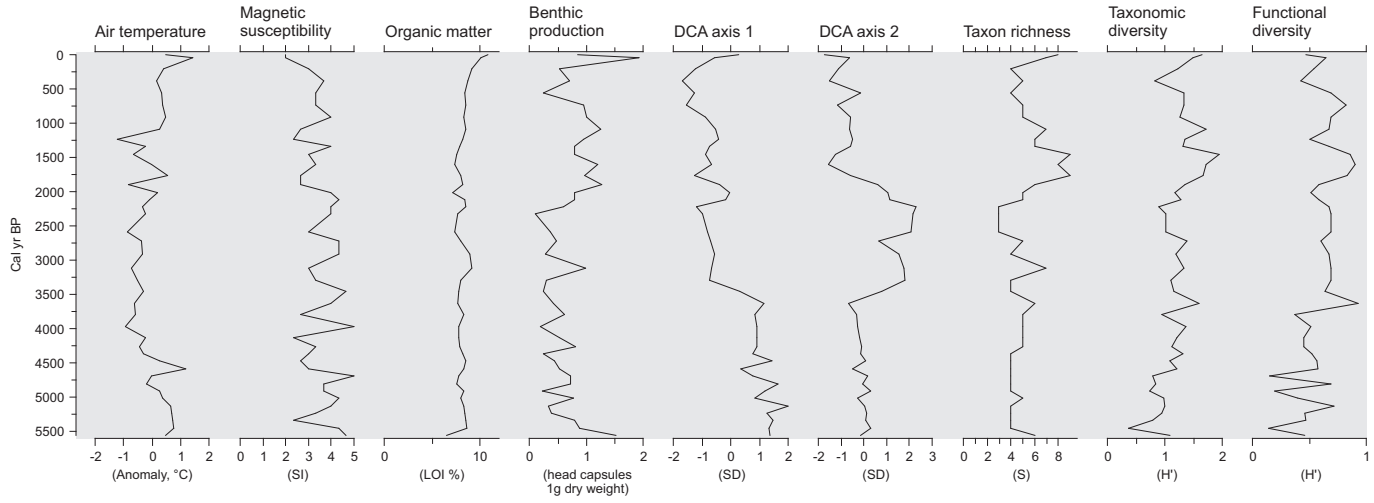

Fig. 7. Svartvatnet record. North Atlantic temperature variability (Sundqvist et al., 2014), magnetic susceptibility and organic matter content (measured as loss on ignition) of the sediment compared with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes scores, taxon richness, taxonomic diversity (Shannon index, H′) and functional diversity of chironomids in the Svartvatnet sediment record.

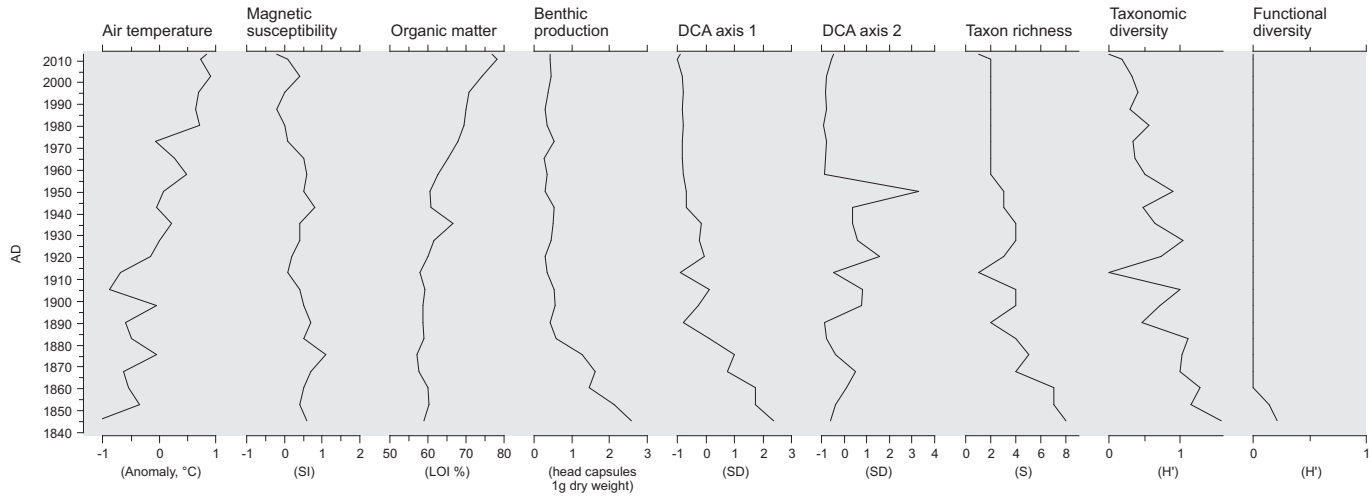

Fig. 8. Fugledammen record. Arctic temperature variability (McKay and Kaufman, 2014), magnetic susceptibility and organic matter content (measured as loss on ignition) of the sediment compared with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes scores, taxon richness, taxonomic diversity (Shannon index, H′) and functional diversity of chironomids in the Fugledammen sediment record.

the environmental stress is released, whereas during press events (e.g. climatic shifts) diversity remains more constant. In the present records, pulse events reflected by magnetic susceptibility do not appear to have distinct influence on the taxonomic or functional diversity of chironomids (Figs. 6–9). The reason for the low influence of pulse disturbances may be that the periglacial catchments have simple characteristics and the lakes are not subjected to direct human impacts or other major pulse event factors, such as volcanic ash deposition (Massaferro and Corley, 1998). However, the climatic press impact on chironomid diversity is clearer as the diversity indices have similar features with climate oscillations.

In the examined temporal records, taxonomic and functional diversity correlate significantly (Fig. 10). In agreement with the present results, long-term taxonomic and functional diversity of aquatic invertebrate communities in the European Alps are closely linked, especially in the case of chironomids (Nevalainen et al., 2015b). The positive relationship between taxon diversity and functional diversity in macroinvertebrates has also been evidenced in contemporary surveys (Feld et al., 2014). Nonetheless, it has also been recently shown that taxonomic and functional turnovers of plants are decoupled in European peat bog ecosystems (Robroek et al., 2017), which partly agrees with our findings from High Arctic lakes. In the oligotrophic sites, the taxonomic and functional changes were concurrent (Figs. 2, 3) but clearly differing in the bird-impacted sites (Figs. 4, 5). In case of peatland plant communities, when species turnover across environmental gradients is restricted to functionally similar species and taxonomic and functional turnovers are decoupled, it allows maintaining ecosystem functioning under environmental change (Robroek et al., 2017). Hence, when turning this general ecological theory around, our results would indicate that when losing chironomid biodiversity, the oligotrophic sites where the taxonomical and functional turnovers are coupled are at greater risk under the ongoing climate change and its future impacts. When benthic functions are reduced, it affects the entire lake ecosystem negatively through simplified food web and inefficient biogeochemical cycling, for example (Jeppesen et al., 2001). This is well illustrated by the bird-impacted sites, where nutrients are recycled from the sediments also due to reduced benthic functions causing internal nutrient enrichment, oxygen depletion in the bottom water, and ecological deterioration (Luoto et al., 2014, 2015).

While using paleoecological data in biodiversity assessments has its benefits (Ilyashuk et al., 2015), the varying level of taxonomic identification of subfossil chironomids should be taken into critical

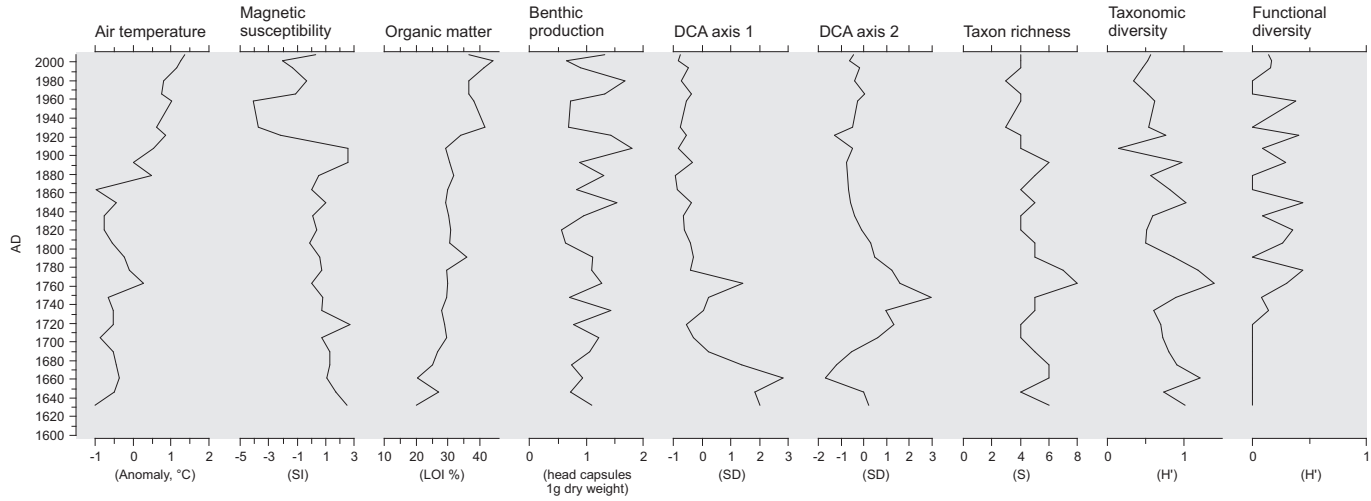

Fig. 9. Kvalroslaguna record Arctic temperature variability (McKay and Kaufman, 2014), magnetic susceptibility and organic matter content (measured as loss on ignition) of the sediment compared with benthic production (total subfossil abundance), detrended correspondence analysis (DCA) axes scores, taxon richness, taxonomic diversity (Shannon index, H′) and functional diversity of chironomids in the Kvalroslaguna sediment record.

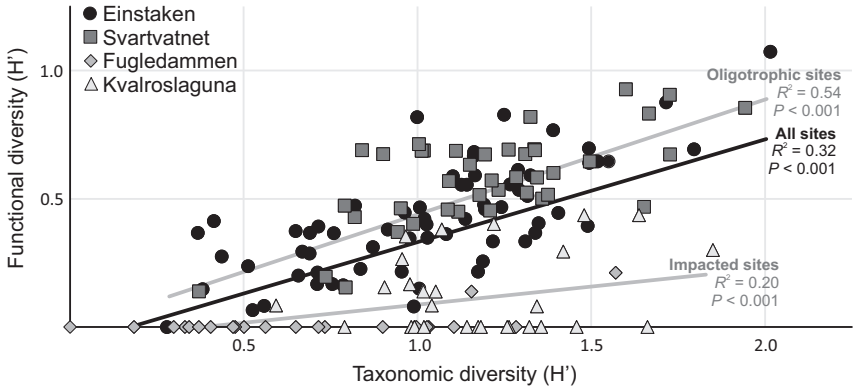

Fig. 10. Linear relationships between taxonomic and functional diversity. Data points are unlabeled core intervals. The oligotrophic sites include Einstaken and Svartvatnet, whereas the bird-impacted sites consist of Fugledammen and Kvalroslaguna.

Table 1
Variance partitioning. Variance explained by forward selected variables (organic matter = loss on ignition, susceptibility = magnetic susceptibility, temperature = surface air temperature anomaly) from the total variance in lakes in Svalbard assessed using constrained redundancy analysis (RDA). Statistically significant variables ($P \leq 0.05$) are marked in bold type.

	Variable	Contribution (%)	*F*	*P*
Einstaken	**Organic matter**	**18.9**	**13.3**	**0.002**
	Susceptibility	**6.5**	**4.9**	**0.004**
	Temperature	**5.3**	**4.2**	**0.002**
Svartvatnet	**Temperature**	**5.6**	**2.3**	**0.050**
	Susceptibility	2.8	1.2	0.308
	Organic matter	1.8	0.7	0.604
Fugledammen	**Temperature**	**25.2**	**7.4**	**0.002**
	Susceptibility	3.3	1.0	0.376
	Organic matter	3.3	1.0	0.392
Kvalroslaguna	**Organic matter**	**17.5**	**5.5**	**0.002**
	Temperature	**5.5**	**1.8**	**0.050**
	Susceptibility	4.3	1.5	0.176

consideration. Although most taxa in the current records were identified to species-type level, there were several taxa that could only be identified at genus level (Figs. 2–5). Therefore, owing to the potential of a genus consisting of more than one species, the biodiversity information may be partly biased, this problem becoming especially important when compared with contemporary datasets using species data. Consequently, the use of functional characterization instead of taxonomic identification may be a more recommendable approach when using subfossil chironomids as a biodiversity measure. This is because the general chironomid feeding preferences do not show notable variability within any genus, with the exception of *Cricotopus*, which includes collector-gatherers, shredders and scrapers (Merritt and Cummins, 1996; Mandaville, 2002). Nonetheless, it should also be noted that most chironomids are omnivorous at some extent and not fully restricted to a single feeding guild.

4.3. Environmental controls on communities

The most important environmental factor controlling chironomid species distribution at the regional scale is air temperature (Heiri et al., 2011; Engels et al., 2014). The effects of climate are also reflected in chironomids via the influence of water temperature, which usually correlate with air temperature (Eggermont and Heiri, 2012). Therefore, the effects of climate are mediated by habitat differences, as well as the physiological effects of water temperature. In our study, despite that the portion of explained variance was relative low, the chironomid assemblage dynamics had significant relationship with temperature in all four sites (Table 1), climate explaining the most significant part of the examined environmental factors in Svartvatnet and Fugledammen. However, detailed comparison with the temperature records probably suffers from chronological biases (chronological matching errors between independent timeseries) compared to the other examined factors (organic matter and magnetic susceptibility), which were analyzed from the sediment profiles and even the same subsamples. Therefore, the correlation between temperature and chironomid communities would most likely be stronger without these chronological issues. In fact, the original study from Svartvatnet (Luoto et al., 2018) showed close correlation between the chironomid dynamics and a temperature reconstruction using a Norwegian (including lakes from Svalbard) chironomid-temperature dataset (Velle et al., 2011). In addition, the chironomid-inferred temperatures were synchronous with an oxygen isotope-based temperature reconstruction from Svartvatnet (Arppe et al., 2017), providing well-built evidence for the close link between chironomids and climate at the study site. The reason why the temperature reconstruction based on the oxygen isotope record was not used in this study was that it was derived from the isotope composition from chironomid head capsules, hence while being independent records, a fully external record (Sundqvist et al., 2014) was selected for the temperature comparisons in this study.

In addition to temperature, limnological factors, such as biological productivity, are known to have major influence on chironomids at the local scale (Brodersen and Quinlan, 2006). Although temperature had a significant role determining the temporal variability in chironomid communities of Einstaken and Kvalroslaguna, the influence of biological production explained a larger part of the dynamics (Fig. 10). Whereas the functional differences in chironomids were clearly related to biological catchment influences (bird impact), the reason behind the differences in community changes between the different geographical locations may be climate-related. Since the Hornsund sites Svartvatnet and Fugledammen are located in southern Svalbard and the Nordaustlandet sites Einstaken and Kvalroslaguna in northernmost Svalbard, there is naturally a significant climate difference (Børre Ørbæk et al., 1999). Therefore, it may be that since the climate in Nordaustlandet has been constantly extremely cold for chironomids throughout the Holocene (i.e. a continuous stable state for cold-adapted chironomids), the limnological effects (i.e., changes in organic matter) explain a larger portion of variability in chironomid assemblages at these colder sites.

Magnetic susceptibility significantly ($P \leq 0.05$) explained temporal chironomid community variability only in Einstaken (Table 1) suggesting that physical changes in catchment properties and the rate of erosion do not play a major role in the chironomid community dynamics of the other three study sites. Aquatic communities in Arctic lakes, which are poorly buffered or have barren catchments may, however, be especially susceptible to catchment greening and changes in hydrology (Schindler and Smol, 2006; Rantala et al., 2017). This is well demonstrated in the present results by the significance of organic

matter in explaining the chironomid communities of the extreme Nordaustlandet sites, which have an open-water season only of ~1 month and catchments with simpler vegetation characteristics. The influence of extreme environmental conditions on chironomids has been well demonstrated also from the European Alps, where major changes in long-term chironomid communities coincided with shifts between different climate regimes and were mainly associated with taxonomic shifts indicating the crossing of ecological thresholds related to ice-cover duration (Ilyashuk et al., 2015). Therefore, ice phenology that also controls the lakes' limnology via the length of biological production and food web development (Quinlan et al., 2005) is probably among the most important environment variables affecting the chironomid assemblages in the High Arctic lakes of Svalbard.

5. Conclusions

The results indicated major ecological turnovers in High Arctic lakes of Svalbard over different temporal scales and clear differences in taxonomic and functional ecology between sites were observed. Taxonomic and functional diversity of chironomids were highest during the early Holocene, when temperatures showed a rapid increase, and in the most recent samples of the oligotrophic sites (Einstaken and Svartvatnet) but not in the bird-impacted sites (Kvalroslaguna and Fugledammen). Climate was a significant explanatory factor in all the sites, whereas biological production (measured as organic matter) was significant in two of the most climatically extreme sites, suggesting that the continuous harsh climate conditions throughout the Holocene and associated short ice-free period and simple catchment characteristics may play a major role in these coldest sites.

The results showed that although taxonomical and functional diversity are always coupled, taxonomic and functional turnovers may be decoupled in certain lakes suggesting that the resilience to future environmental change is site-specific, especially if functional redundancy is lost. In particular, the oligotrophic sites appear to be at greater risk under the ongoing climate change. It also appears that functional diversity in sediment records well-explained environmental conditions in lakes, and consequently has great potential in environmental change paleoreconstructions, which can be used also to understand future changes.

Acknowledgements

This work was supported by the Academy of Finland (grant numbers 1116509 and 259343) and the Emil Aaltonen Foundation (grant numbers 160156 and 170161). Comments by two anonymous reviewers helped to improve the manuscript.

References

Arppe, L., Kurki, E., Wooller, M.J., Luoto, T.P., Zajączkowski, M., Ojala, A.E.K., 2017. A 5500-year oxygen isotope record of high-arctic environmental change from southern Spitsbergen. The Holocene 27, 1948–1962.
Belle, S., Luoto, T.P., Kivilä, E.H., Nevalainen, L., 2017. Chironomid paleo diet as an indicator of past carbon cycle in boreal lakes: Lake Kylmänlampi (Kainuu province; Eastern Finland) as a case study. Hydrobiologia 785, 149–158.
Berg, M.B., 1995. Larval food and feeding behaviour. In: Armitage, P.D., Cranston, P.S., Pinder, L.C.V. (Eds.), The Chironomidae. Springer, Dordrecht, pp. 136–168.
Børre Ørbæk, J., Hisdal, V., Edin Svaasand, L., 1999. Radiation climate variability in Svalbard: surface and satellite observations. Polar Res. 18, 127–134.
Brodersen, K.P., Quinlan, R., 2006. Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. Quat. Sci. Rev. 25, 1995–2012.
Brooks, S.J., Birks, H.J.B., 2004. The dynamics of Chironomidae (Insecta: Diptera) assemblages in response to environmental change during the past 700 years on Svalbard. J. Paleolimnol. 31, 483–498.
Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The Identification and Use of Palaeoarctic Chironomidae Larvae in Palaeoecology. QRA Technical Guide No. 10. Quaternary Research Association, London.
Burgmer, T., Hillebrand, H., Pfenninger, M., 2007. Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151, 93–103.
Cadotte, M.V., Carscadden, K., Mirotchnik, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48, 1079–1087.
Correa-Metrio, A., Dechnik, Y., Lozano-García, S., Caballero, M., 2014. Detrended correspondence analysis: a useful tool to quantify ecological changes from fossil data sets. Bol. Soc. Geol. Mex. 66.
Covich, A.P., Palmer, M.A., Crowl, T.A., 1999. The role of benthic invertebrate species in freshwater ecosystems. Bioscience 49, 119–127.
Cummins, K.W., 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 2418, 183–206.
Dearing, J.A., 1999. Holocene environmental change from magnetic proxies in lake sediments. In: Maher, B.A., Thompson, R. (Eds.), Quaternary Climates, Environments and Magnetism. Cambridge University Press, pp. 231–278.
Eggermont, H., Heiri, O., 2012. The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. Biol. Rev. 87, 430–456.
Engels, S., Self, A.E., Luoto, T.P., Brooks, S.J., Helmens, K.F., 2014. A comparison of three Eurasian chironomid-climate calibration datasets on a W-E continentality gradient and the implications for quantitative temperature reconstructions. J. Paleolimnol. 51, 529–547.
Feld, C.K., de Bello, F., Dolédec, S., 2014. Biodiversity of traits and species both show weak response to hydromorphological alteration in lowland river macroinvertebrates. Freshw. Biol. 59, 233–248.
Fortin, M.C., Gajewski, K., 2010. Holocene climate change and its effect on lake ecosystem production on northern Victoria Island, Canadian Arctic. J. Paleolimnol. 43, 219–234.
Fournier, B., Lara, E., Jassey, V.E., Mitchell, E.A., 2015. Functional traits as a new approach for interpreting testate amoeba palaeo-records in peatlands and assessing the causes and consequences of past changes in species composition. The Holocene 25, 1375–1383.
Frey, D.G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. J. Paleolimnol. 3, 179–191.
Gregory-Eaves, I., Beisner, B.E., 2011. Palaeolimnological insights for biodiversity science: an emerging field. Freshw. Biol. 56, 2653–2661.
Grey, J., Kelly, A., Ward, S., Sommerwerk, N., Jones, R.I., 2004. Seasonal changes in the stable isotope values of lake-dwelling chironomid larvae in relation to feeding and life cycle variability. Freshw. Biol. 49, 681–689.
van Hardenbroek, M., Lotter, A.F., Bastviken, D., Andersen, T.J., Heiri, O., 2014. Taxon-specific $\delta^{13}C$ analysis of chitinous invertebrate remains in sediments from Strandsjön, Sweden. J. Paleolimnol. 52, 95–105.
Heiri, O., Brooks, S.J., Birks, H.J.B., Lotter, A.F., 2011. A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. Quat. Sci. Rev. 30, 3445–3456.
Ilyashuk, E.A., Ilyashuk, B.P., Tylmann, W., Koinig, K.A., Psenner, R., 2015. Biodiversity dynamics of chironomid midges in high-altitude lakes of the Alps over the past two millennia. Insect Conserv. Diver. 8, 547–561.
Isaksen, K., Benestad, R.E., Harris, C., Sollid, J.L., 2007. Recent extreme near-surface permafrost temperatures on Svalbard in relation to future climate scenarios. Geophys. Res. Lett. 34.
Itkonen, A., Marttila, V., Meriläinen, J., Salonen, V.-P., 1999. 8000-year history of palaeoproductivity in a large boreal lake. J. Paleolimnol. 21, 271–294.
Jensen, T.C., Dimante-Deimantovica, I., Schartau, A.K., Walseng, B., 2013. Cladocerans respond to differences in trophic state in deeper nutrient poor lakes from Southern Norway. Hydrobiologia 715, 101–112.
Jeppesen, E., Leavitt, P., De Meester, L., Jensen, J.P., 2001. Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. Trends Ecol. Evol. 16, 191–198.
Keatley, B.E., Douglas, M.S., Blais, J.M., Mallory, M.L., Smol, J.P., 2009. Impacts of seabird-derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island, Canadian High Arctic. Hydrobiologia 621, 191–205.
Levesque, A.J., Cwynar, L.C., Walker, I.R., 1996. Richness, diversity and succession of late-glacial chironomid assemblages in New Brunswick, Canada. J. Paleolimnol. 16, 257–274.
Linderholm, H.W., Nicolle, M., Francus, P., Gajewski, K., Helama, S., Korhola, A., Solomina, O., Yu, Z., Zhang, P., D'Andrea, W.J., Debret, M., Divine, D., Gunnarson, B.E., Loader, N.J., Massei, N., Seftifgen, K., Thomas, E.K., Werner, J., Andersson, S., Berntsson, A., Luoto, T.P., Nevalainen, L., Saarni, S., Väliranta, M., 2018. Arctic hydroclimate variability during the last 2000 years: current understanding and research challenges. Clim. Past 14, 473–514.
Liu, X.Q., Wang, H.Z., 2008. Food web of benthic macroinvertebrates in a large Yangtze River-connected lake: the role of flood disturbance. Fundam. Appl. Limnol. 171, 297–309.
Luoto, T.P., 2011. The relationship between water quality and chironomid distribution in Finland – a new assemblage-based tool for assessments of long-term nutrient dynamics. Ecol. Indic. 11, 255–262.
Luoto, T.P., Nevalainen, L., 2015. Climate-forced patterns in midge feeding guilds. Hydrobiologia 742, 141–152.
Luoto, T.P., Ojala, A.E.K., 2014. Paleolimnological assessment of ecological integrity and eutrophication history for Lake Tiiläänjärvi (Askola, Finland). J. Paleolimnol. 51, 455–468.
Luoto, T.P., Nevalainen, L., Kubischta, F., Kultti, S., Knudsen, K.L., Salonen, V.-P., 2011. Late quaternary ecological turnover in high arctic Lake Einstaken, Nordaustlandet, Svalbard (80° N). Geogr. Ann. A 93, 337–354.
Luoto, T.P., Brooks, S.J., Salonen, V.-P., 2014. Ecological responses to climate change in a bird-impacted High Arctic pond (Nordaustlandet, Svalbard). J. Paleolimnol. 51, 87–97.
Luoto, T.P., Oksman, M., Ojala, A.E.K., 2015. Climate change and bird impact as drivers of High Arctic pond deterioration. Polar Biol. 38, 357–368.
Luoto, T.P., Oksman, M., Ojala, A.E.K., 2016. Invertebrate communities of the High Arctic

ponds in Hornsund. Pol. Polar Res. 37, 105–119.
Luoto, T.P., Ojala, A.E.K., Arppe, L., Brooks, S.J., Kurki, E., Oksman, M., Wooller, M.J., Zajączkowski, M., 2018. Synchronized proxy-based temperature reconstructions reveal mid- to late Holocene climate oscillations in High Arctic Svalbard. J. Quat. Sci. 33, 93–99.
Majewski, W., Szczuciński, W., Zajączkowski, M., 2009. Interactions of Arctic and Atlantic water-masses and associated environmental changes during the last millennium, Hornsund (SW Svalbard). Boreas 38, 529–544.
Mandaville, S.M., 2002. Benthic macroinvertebrates in freshwaters—taxa tolerance values, metrics, and protocols. In: Soil & Water Conservation Society of Metro Halifax.
Massaferro, J., Corley, J., 1998. Environmental disturbance and chironomid palaeodiversity: 15 kyr BP of history at Lake Mascardi, Patagonia, Argentina. Aquat. Conserv. Mar. Freshwat. Ecosyst. 8, 315–323.
McKay, N.P., Kaufman, D.S., 2014. An extended Arctic proxy temperature database for the past 2,000 years. Sci. Data 1, 140026.
Merritt, R.W., Cummins, K.W. (Eds.), 1996. An Introduction to the Aquatic Insects of North America. Kendall-Hunt, Dubuque.
Meyers, P.A., Lallier-Verges, E., 1999. Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. J. Paleolimnol. 21, 345–372.
Meyers, P.A., Teranes, J.L., 2002. Sediment organic matter. In: Tracking Environmental Change Using Lake Sediments, pp. 239–269.
Nevalainen, L., Luoto, T.P., 2017. Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients. Funct. Ecol. 31, 488–498.
Nevalainen, L., Van Damme, K., Luoto, T.P., Salonen, V.-P., 2012. Fossil remains of an unknown Alona species (Chydoridae, Aloninae) from a high arctic lake in Nordaustlandet (Svalbard) in relation to glaciation and Holocene environmental history. Polar Biol. 35, 325–333.
Nevalainen, L., Rantala, M.V., Luoto, T.P., 2015a. Sedimentary cladoceran assemblages and their functional attributes record late Holocene climate variability in southern Finland. J. Paleolimnol. 54, 239–252.
Nevalainen, L., Luoto, T.P., Manca, M., Weisse, T., 2015b. A paleolimnological perspective on aquatic biodiversity in Austrian mountain lakes. Aquat. Sci. 77, 59–69.
Nevalainen, L., Brown, M., Manca, M., 2018. Sedimentary record of cladoceran functionality under eutrophication and re-oligotrophication in Lake Maggiore, northern Italy. WaterSA 10, 86.
Nyman, M., Korhola, A., Brooks, S.J., 2005. The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. Glob. Ecol. Biogeogr. 14, 137–153.
Ojala, A.E.K., Arppe, L., Luoto, T.P., Wacker, L., Kurki, E., Zajączkowski, M., Pawłowska, J., Damrat, M., Oksman, M., 2016. Sedimentary environment, lithostratigraphy and dating of sediment sequences from Arctic lakes Revvatnet and Svartvatnet in Hornsund, Svalbard. Pol. Polar Res. 37, 23–48.
Palmer, M.A., Covich, A.P., Finlay, P.J., et al., 1997. Biodiversity and ecosystem processes in freshwater sediments. Ambio 26, 571–577.
Paull, T.M., Finkelstein, S.A., Gajewski, K., 2017. Interactions between climate and landscape driven Holocene ecological change in a High Arctic lake on Somerset Island, Nunavut, Canada. Arctic Sci. 3, 17–38.
Pinder, L.C.V., 1986. Biology of freshwater Chironomidae. Annu. Rev. Entomol. 31, 1–23.
Pla-Rabes, S., Flower, R.J., Shilland, E.M., Kreiser, A.M., 2011. Assessing microbial diversity using recent lake sediments and estimations of spatio-temporal diversity. J. Biogeogr. 38, 2033–2040.
Quinlan, R., Douglas, M.S., Smol, J.P., 2005. Food web changes in arctic ecosystems related to climate warming. Glob. Chang. Biol. 11, 1381–1386.
Rantala, M.V., Luoto, T.P., Weckström, J., Rautio, M., Nevalainen, L., 2017. Climate drivers of diatom distribution in shallow subarctic lakes. Freshw. Biol. 62, 1971–1985.
Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W.F., Christoffersen, K.S., 2011. Shallow freshwater ecosystems of the circumpolar Arctic. Ecoscience 18, 204–222.
Robroek, J.M., Jassey, V.E.J., Payne, R.J., et al., 2017. Taxonomic and functional turnover are decoupled in European peat bogs. Nat. Commun. http://dx.doi.org/10.1038/s41467-017-01350-5.
Royall, D., 2001. Use of mineral magnetic measurements to investigate soil erosion and sediment delivery in a small agricultural catchment in limestone terrain. Catena 46, 15–34.
Sandgren, P., Snowball, I., 2002. Application of mineral magnetic techniques to paleolimnology. In: Tracking Environmental Change Using Lake Sediments. Springer, Netherlands, pp. 217–237.
Schilder, J., van Hardenbroek, M., Bodelier, P., Kirilova, E.P., Leuenberger, M., Lotter, A.F., Heiri, O., 2017. Trophic state changes can affect the importance of methane-derived carbon in aquatic food webs. Proc. R. Soc. B 284, 20170278.
Schindler, D.W., Smol, J.P., 2006. Cumulative effects of climate warming and other human activities on freshwaters of Arctic and subarctic North America. Ambio 35, 160–168.
Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80, 469–484.
Schmera, D., Heino, J., Podani, J., Erős, T., Dolédec, S., 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787, 27–44.
Serreze, M.C., Barry, R.G., 2011. Processes and impacts of Arctic amplification: a research synthesis. Glob. Planet. Chang. 77, 85–96.
Shala, S., Helmens, K.F., Luoto, T.P., Väliranta, M., Weckström, J., Salonen, J.S., Kuhry, P., 2014. Evaluating environmental drivers of Holocene changes in water chemistry and aquatic biota composition at Lake Loitsana. NE Finland. J. Paleolimnol. 52, 311–329.
Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27 (379–423), 623–656.
Šmilauer, P., Lepš, J., 2014. Multivariate Analysis of Ecological Data Using CANOCO 5. Cambridge University Press.
Smol, J.P., 2010. The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. Freshw. Biol. 55, 43–59.
Smol, J.P., Douglas, M.S., 2007. From controversy to consensus: making the case for recent climate change in the Arctic using lake sediments. Front. Ecol. Environ. 5, 466–474.
Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. J. N. Amer. Benthol. Soc. 29, 344–358.
Sundqvist, H.S., Kaufman, D.S., McKay, N.P., et al., 2014. Arctic Holocene proxy climate database - new approaches to assessing geochronological accuracy and encoding climate variables. Clim. Past 10, 1605–1631.
Vadeboncoeur, Y., Vander Zanden, M.J., Lodge, D.M., 2002. Putting the Lake back together: reintegrating benthic pathways into Lake food web models: Lake ecologists tend to focus their research on pelagic energy pathways, but, from algae to fish, benthic organisms form an integral part of lake food webs. AIBS Bull. 52, 44–54.
Velle, G., Kongshavn, K., Birks, H.J.B., 2011. Minimizing the edge-effect in environmental reconstructions by trimming the calibration set: chironomid-inferred temperatures from Spitsbergen. The Holocene 21, 417–430.
Wrona, F.J., Johansson, M., Culp, J.M., et al., 2016. Transitions in Arctic ecosystems: ecological implications of a changing hydrological regime. J. Geophys. Res. Biogeosci. 121, 650–674.